

THE INTERPRETATION OF SIZE-FREQUENCY DISTRIBUTIONS IN MOLLUSCAN DEATH ASSEMBLAGES

by A. HALLAM

ABSTRACT. It has been widely assumed that water currents play a major role in determining the shape of the size-frequency distributions of molluscan and brachiopod shells in death assemblages, by the selective removal of small-size grades. To test this assumption, the commonest bivalve and gastropod species in two transported death assemblages, one fossil and one forming at present, have been subjected to size-frequency analysis. The interaction of varying growth and mortality rates among living bivalves is discussed and the results of experimental work on shell fragmentation presented. It is concluded that the size-frequency distributions of the death assemblages under consideration primarily reflect growth and mortality rates, modified somewhat by the selective destruction of smaller shells. The invocation of size sorting appears to be unnecessary, and this postulated process has still to be demonstrated as a significant factor in controlling the shape of size-frequency distributions.

A RECENT palaeoecological paper by Fagerstrom (1964) contains the following statement (p. 1202): 'Large areas of the sea floor are swept by relatively weak currents of low competence. In these areas the small empty shells of the uncemented benthonic and pelagic species are removed by currents; the residue consists mostly of large shells which, upon burial, become residual fossil communities. The effect of this selective removal of larger numbers of small, empty shells is to change right-skewed (i.e. positively skewed) size-frequency distributions of unwinnowed populations to distributions that are bell-shaped or normal. . . . The location of the mode depends largely on the competence of the current.' These assertions express a common belief in the importance of size sorting by water currents, which was reinforced by the theoretical work of Boucot (1953) and Olson (1957). This belief lacks, however, a sound basis in empirical observations and has been contested for particular instances by Craig and Hallam (1963) and Broadhurst (1964).

A primary object of this paper is to investigate the validity of Fagerstrom's ideas with reference to two concentrations of molluscan shells (or shell beds), one forming at the present, the other fossil, which have been undoubtedly affected by strong current activity. Both beds contain the young and adult shells of a large number of species of widely varying size. If size sorting is as important a factor as has been claimed it should have had a major effect on the size distributions.

The influence on size-frequency distributions of varying growth and mortality rates and of selective fragmentation of shells is also considered.

DESCRIPTION OF SHELL CONCENTRATIONS

Newport Bay, southern California

The lower terrace in the upper part of the bay contains an extremely fossiliferous Upper Pleistocene shell bed. Approximately fifty species, predominantly bivalves and gastropods, occur in a matrix of shell fragments and coarse sand with scattered stone

cobbles, encrusted with serpulids, bryozoans, and barnacles. Most of the shells are fresh and well-preserved but a few apparently reworked shells occur, notably a species of *Cardita*.

A sample was collected from a part of the shell bed several yards in area and 2 ft. deep. This sample was subsequently screened through a 1-mm. mesh sieve and complete shells separated from fragmentary material by hand picking.

The commonest bivalves of large size were *Tivela stultorum*, *Clinocardium nuttali*, *Chlamys hastatus hericius*, and *Pseudochama exogyra*, but small-sized species are much more abundant. Disarticulation was complete. The numbers of right and left valves were compared for two of the commonest occurring species, both of the genus *Donax*, and also for a species of *Tellina*(?). There were 408 left and 426 right valves of *Donax gouldi*. The corresponding figures for *D. californica* are 255 and 211 and for *Tellina*(?) *sp.* 107 and 86. Application of the Chi-Square (χ^2) test showed that there is a significant difference at the 5% level in the case of *Donax californica*.

Separate plots of the size frequency distributions of both right and left valves of the *Donax* species give similar results. Therefore in the case of the other bivalve species selected for study, the two valves have not been separated. Only ten species of bivalves and gastropods were sufficiently abundant in the sample to give satisfactory size-frequency histograms (text-fig. 1). Measurements of the maximum dimension were made to the nearest millimetre but are given in terms of pairs of millimetres, as in Craig and Hallam (1963).

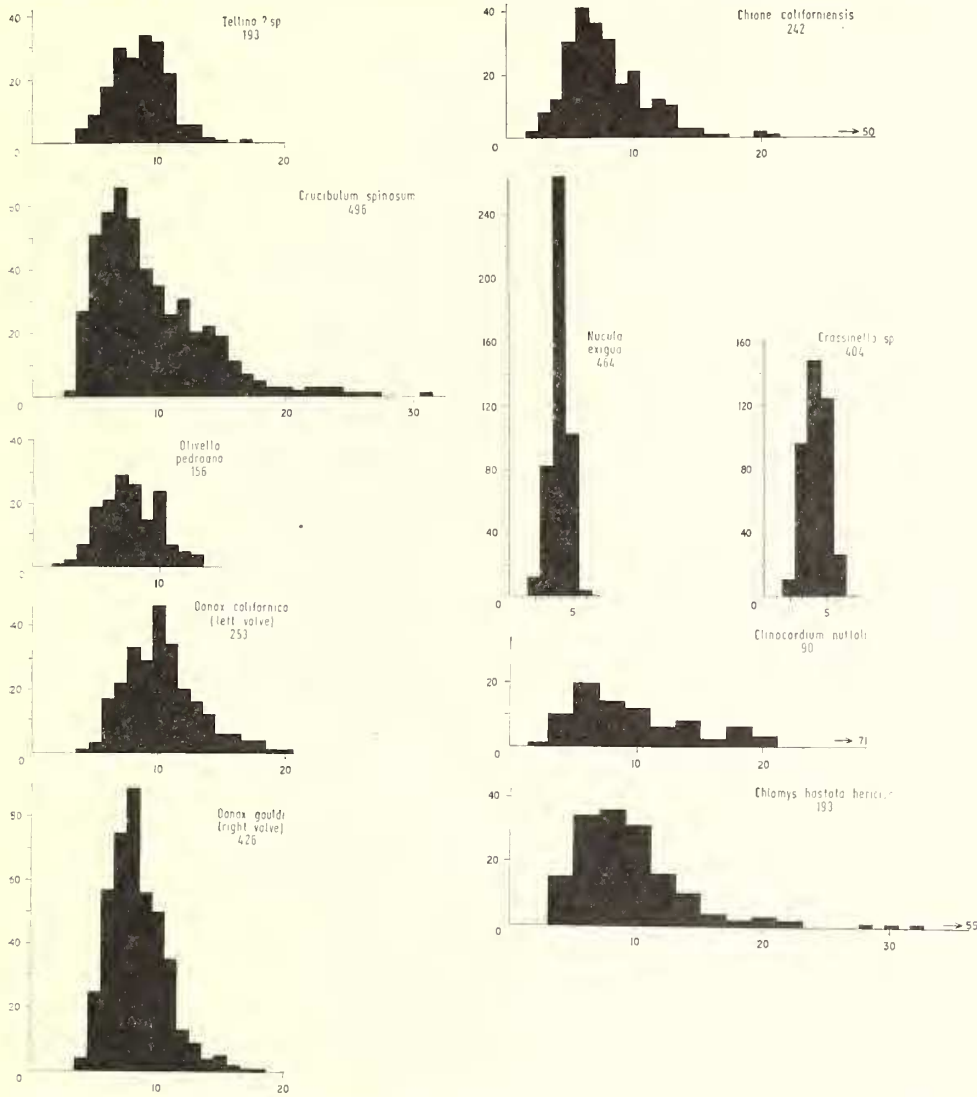
In the comparison of size-frequency distributions of species of widely varying size the straightforward plotting of numbers against length in millimetres is not entirely satisfactory. To bring such distributions more into line, it is better to express size as a percentage of the maximum. In text-fig. 2 the measurements have been grouped into six frequency classes, the class interval being defined for each sample as one-sixth of the maximum value observed in the sample. This method of plotting demands large samples of given species, since otherwise major inaccuracies might arise in determining the maximum size. Another disadvantage is that large species are represented by cruder histograms than small ones. Clearly, grouping into such frequency classes should only be used to supplement histograms of the more orthodox kind.

Text-figs. 1 and 2 indicate that the histograms may be divided into three groups: (a) those with a strong positive skewness (*Clinocardium*, *Chlamys*, *Chione*); (b) those with a moderate positive skewness (both *Donax* species, *Tellina*, *Crucibulum*); (c) those that are more or less symmetrical (*Olivella*, *Nucula*, *Crassinella*). It is likely, however, that the distributions of the last two bivalves are distorted, since a large proportion of these minute shells must have escaped through the 1-mm. mesh sieve. The purpose in plotting histograms in these cases will become apparent later. *Tivela* and *Pseudochama* were at least as abundant as *Chlamys* and *Clinocardium* in the largest size grades of the shell bed but were poorly represented in the sample because of a paucity of small shells.

Gosford Bay, East Lothian, Scotland

A sample containing at least twenty-five species of bivalves and gastropods was collected from an area of several square yards near high-tide mark in the middle of Gosford Bay. The rich shell accumulation at this level of the beach, containing much broken shell material, occurs in a matrix of medium sand with small pebbles of basalt derived from

nearby reefs. As before, the sample was sieved (this time with a 2-mm. mesh sieve) and complete shells separated from fragments and grouped into species.



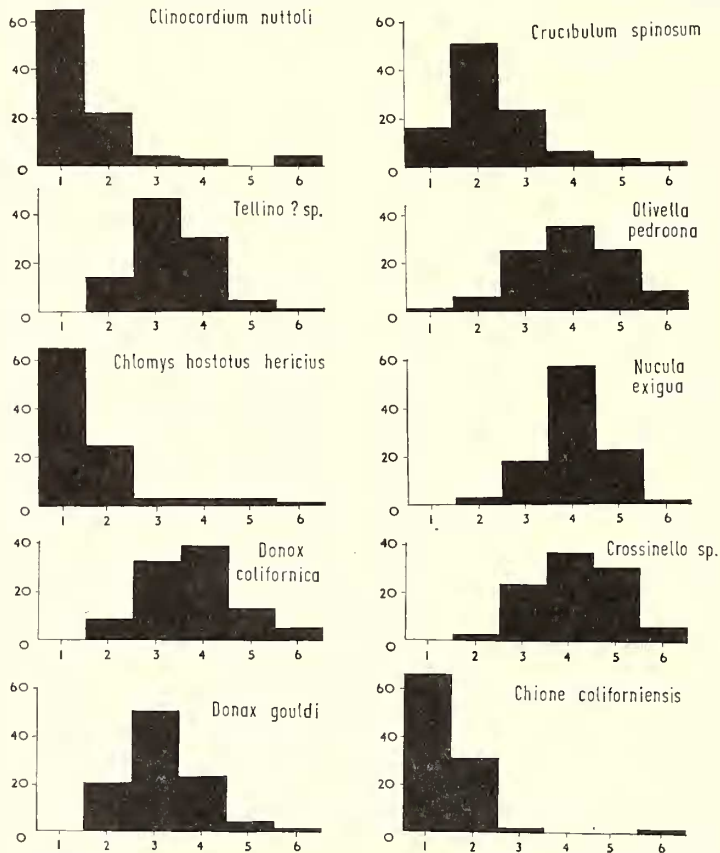
TEXT-FIG. 1. Size-frequency distributions of molluscan species from Newport Bay assemblage. Size (in mm.) along abscissa.

Disarticulation of the bivalves was complete, with the exception of a few young specimens of *Mytilus edulis*. The distribution of numbers of left and right valves among the commonest species is as follows:

	<i>Left valves</i>	<i>Right valves</i>
<i>Cardium edule</i>	57	64
<i>Macoma baltica</i>	31	29
<i>Mytilus edulis</i>	200	218
<i>Venus fasciata</i>	33	30

Application of the Chi-Square (χ^2) test revealed no significant difference for any of these species.

Text-fig. 3 gives the size-frequency distributions of the commonest species in the sample, with the exception of *Littorina littorea*. This was excluded because of the difficulty of effecting a rigorous separation from two other *Littorina* species, *L. saxatilis* and *L. neritoides*. *L. littorea* is undoubtedly by far the most abundant of the three, however,



TEXT-FIG. 2. Size-frequency distributions of the same species as in text-fig. 1, plotted in terms of six frequency classes.

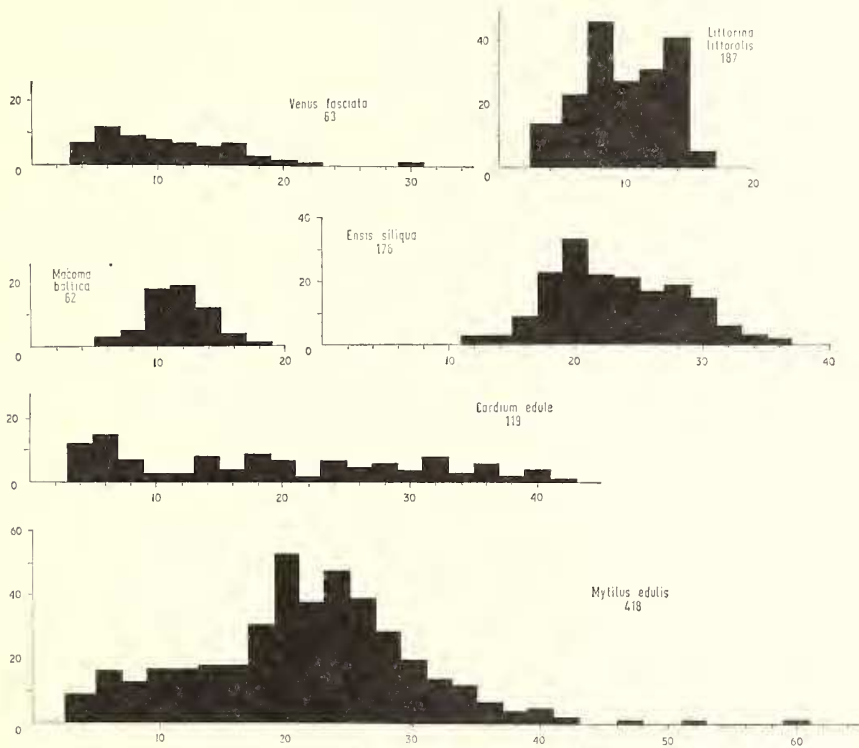
and an approximate idea of its size-frequency distribution can be obtained from text-fig. 8, in which all three species are grouped together. All species are plotted in terms of maximum size except for *Ensis siligna*. This species is so much larger than the others in the sample that it was convenient to plot width rather than length. These two measures are related by an approximate ratio of 1:7.

In text-fig. 4 these data are plotted as in text-fig. 2, and the same treatment is applied to previously published size-frequency data on *Cardium* and *Mytilus* collected from similar death assemblages (Craig and Hallam 1963).

Numbers being smaller than in the Newport Bay sample, it is not surprising that the histograms are less regular. Nevertheless, it is apparent that moderate positive skewness

is again dominant, with *Macoma* and *Ensis* approaching most closely to a symmetrical shape. The *Mytilus* sample of Gosford Bay differs from those of Fernie Ness and Craigelaw Bay principally in the greater proportion of small forms. The *Littorina* histograms differ from all others in being clearly bimodal.

It is instructive to plot the position of the histogram modes for both samples against number of the frequency class in text-figs. 2 and 4. Text-fig. 5 shows that there is a maxi-



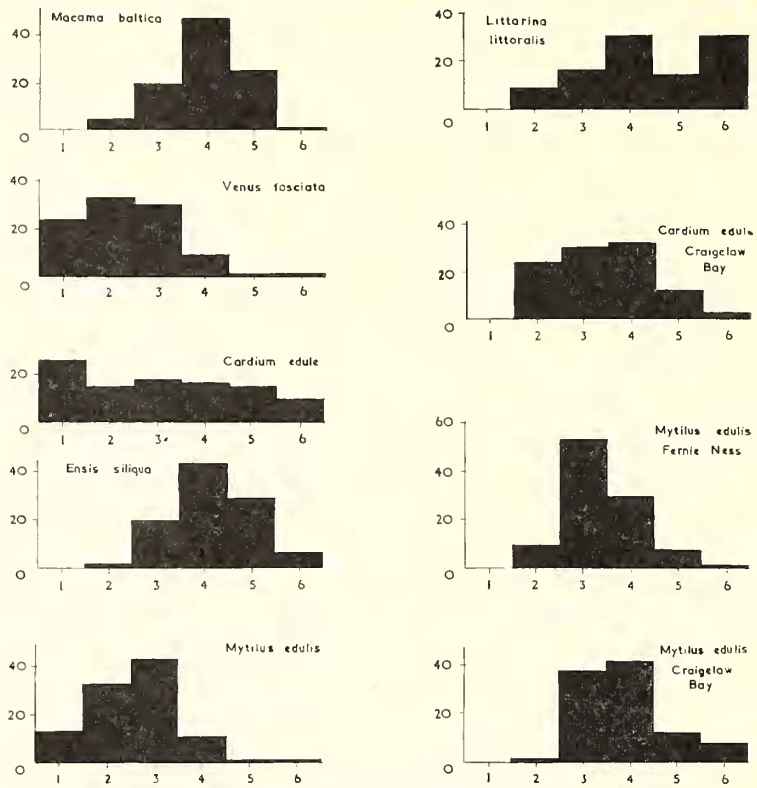
TEXT-FIG. 3. Size-frequency distributions of molluscan species from Gosford Bay assemblage. Size in mm.

mum at the fourth and a slight rise towards the first such class. Except for the anomalous *Littorina* distribution, there are no modes at the fifth or sixth. To summarize the principal size-frequency characteristics in the two samples, strong positive skewness and symmetrical distributions are less common than moderate positive skewness, and negative skewness is absent.

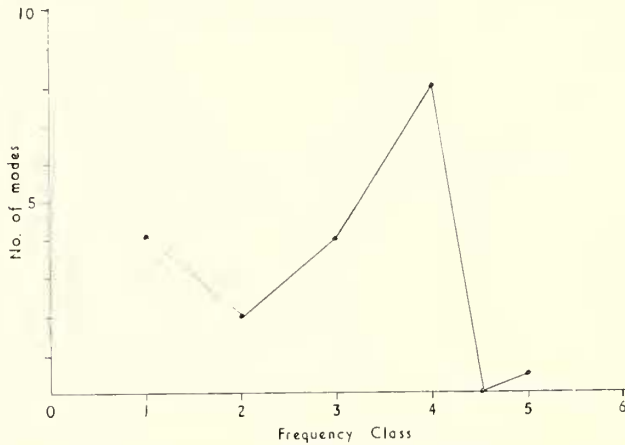
The anomalous bimodal distribution of *Littorina littoralis* in the Gosford Bay sample is readily explained by the occurrence of a living community of this species a few yards away on a rocky reef. Unlike the other species in the sample, most *Littorina* shells have been transported very little distance, and the death assemblage evidently reflects the sudden death of a large number of individuals of more than one age group.

Both shell assemblages were clearly transported to their present positions by water movements and laid down in highly disturbed conditions. The data presented here do not support the contention that size sorting is the primary agent in shaping the

size-frequency distributions. Symmetrical bell-shaped distributions are exceptional and the hypothesis of size sorting offers no explanation of the widely differing size distribu-



TEXT-FIG. 4. Size-frequency distributions of the same species as in text-fig. 3, plotted as in text-fig. 2.



TEXT-FIG. 5. Plot of modal number of frequency class, of species in Newport and Gosford Bay assemblages. Explanation in text.

tions of species of similar size in the same sample, such as the Gosford Bay *Macoma* and *Venus*, and the Newport Bay *Tivela* and *Clinocardium*, nor for the very similar size distributions of certain small and large species of the same sample. It does not seem plausible to attribute the rarity or absence of small shells of large species to removal by currents when shells of other, small species occur in abundance in the same sample. This is strikingly true of both samples. In that from Newport Bay, minute species of *Nucula* and *Crassinella* occur in huge quantities within the size grades 1–5 mm, which are thinly represented in some of the larger species. Similarly, although the Gosford Bay sample contains abundant shells of less than 10 mm length there is a complete absence of the large and elongate *Ensis* species in this size grade, even when only width measurements are taken into account. (The data are even more striking, of course, if length is considered.)

Interpretation of the size-frequency distributions is impossible without an adequate understanding of the interaction of varying growth and mortality rates, and attention must now turn to this topic.

GROWTH AND MORTALITY RATES IN LIVING BIVALVES

Data on growth and mortality rates are much more abundant for bivalves than gastropods and attention will be confined here to the former. Such data as exist give no reason for supposing that gastropods are appreciably different in these respects.

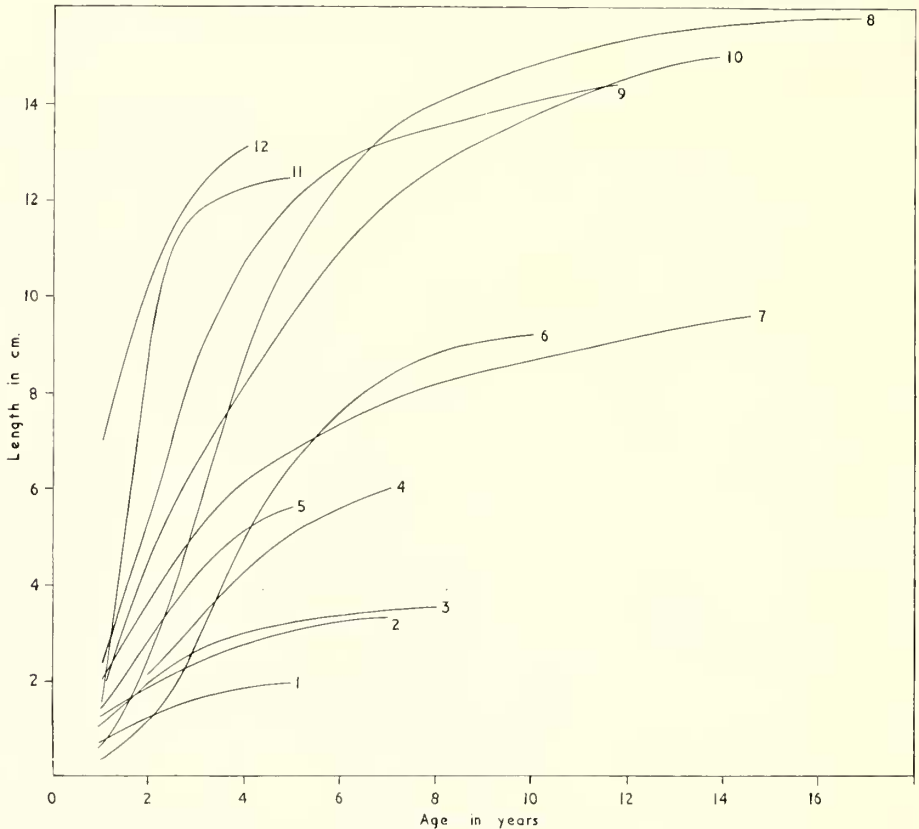
Growth rates. The annual growth of bivalve shells can be determined by growth-ring analysis, each ring corresponding to a year. The reliability of this technique has been established by direct observation by many workers (e.g. Weymouth 1923, Weymouth *et al.* 1925, Orton 1926, Newcombe 1935, Mason 1957). Complications due to disturbance rings can usually be eliminated by taking average results from large samples. Data for a number of representative bivalves have been plotted in text-fig. 6. This should be studied in conjunction with Table 1, which gives the source of the information for each species.

TABLE 1

1. <i>Cardium edule</i>	(Orton 1926)
2. <i>Cardium edule</i>	(Vogel 1959)
3. <i>Venus gallina</i>	(Vogel 1959)
4. <i>Mya arenaria</i>	(Newcombe 1935)
5. <i>Mytilus edulis</i>	(Savage 1956)
6. <i>Cardium corbis</i>	(Weymouth and Thompson 1931)
7. <i>Venus merceuarina</i>	(Hopkins 1930)
8. <i>Siliqua patula</i> , Alaska	(Weymouth <i>et al.</i> 1931)
9. <i>Pecten maximus</i>	(Mason 1957)
10. <i>Tivela stultorum</i>	(Weymouth 1923)
11. <i>Siliqua patula</i> , California	(Weymouth <i>et al.</i> 1931)
12. <i>Mytilus californianus</i>	(Coe and Fox 1944)

It will be seen that in general there is a steady decline in rate of growth with age, though it never completely ceases during life. Careful work by Weymouth *et al.* (1931) on the Pacific razor clam *Siliqua patula* has shown that the growth cannot be expressed accurately by a simple exponential function. Such a function fails to account both for the characteristic sigmoid shape of the growth curve, with a point of inflection near the origin, and for the growth of the oldest clams, which is greater than calculated. Growth

is, indeed, an exponential function of time, but the exponent is a changing one, decreasing with time in an exponential fashion. The inflection appears in fact to have no independent biological significance. It is likely that the study of Weymouth and his co-workers has a fairly general application to bivalves, since sigmoidal growth curves are not uncommon.



TEXT-FIG. 6. Simplified graphical plot of growth data for twelve species of bivalves. See Table 1.

Another point brought out in this important study is that in low latitudes a relatively high growth rate is combined with relatively early death. In high latitudes growth is slower because of lower temperatures and hence lower metabolic rates, but longevity and the ultimate size attained are greater. Intermediate latitudes show correspondingly intermediate growth and mortality characteristics. The bearing of data of this type on the problem of stunting has already been discussed elsewhere (Hallam 1965); it remains to be noted here that where growth-ring analysis is feasible, there seems to be a promising prospect of working out palaeotemperature gradients if fossil material is collected from the same horizon over a large area. Much more work is required, however, on other Recent species to determine whether these relationships have a general application.

Mortality rates. It is quite evident that larval mortality in bivalves must be enormous but, as pointed out by Craig and Hallam (1963), this can be disregarded by palaeoecologists,

who are only concerned with fossilizable material. Therefore the only relevant mortality rates are those following the successful settling of spat. Data are unfortunately scant as yet, but examination of the literature and correspondence with marine biologists has revealed one case where there is sufficient information available for the construction of an adequate life table and survivorship curve. The Californian Pismo Clam, *Tivela stultorum*, has considerable economic importance and hence has received detailed study over a long period. Biological knowledge of this species was summarized by Fitch (1950), who gave mortality data based on a census taken over several years. A life table has been constructed (Table 2) with these basic data, using a method of calculation proposed

TABLE 2

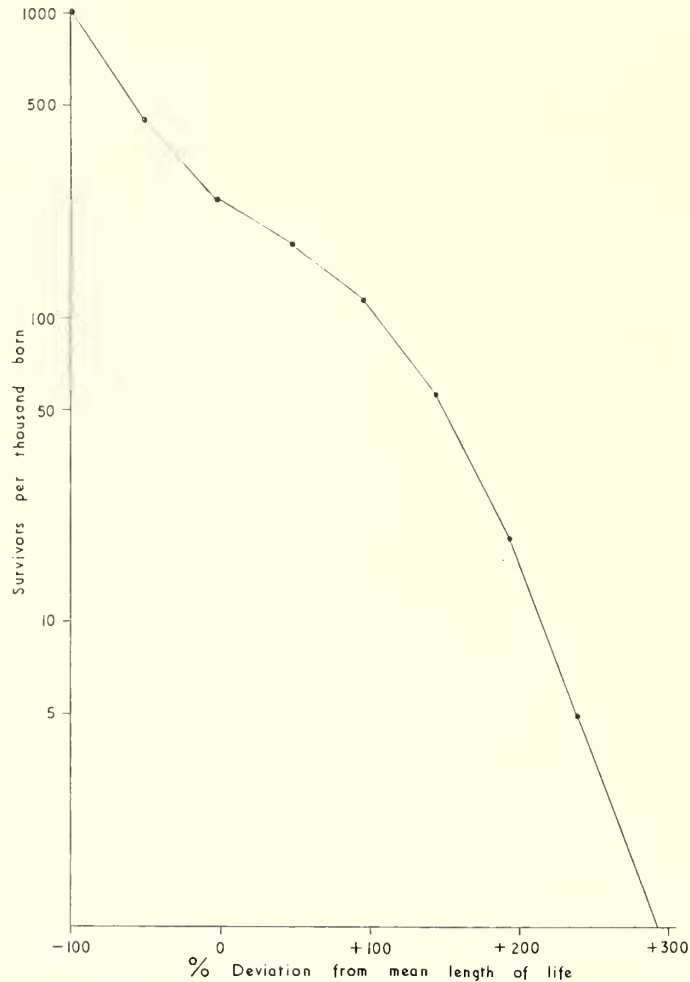
Age (years)	Age as % deviation from mean length of life	Number dying in age interval out of 1,000 born	Number surviving at beginning of age interval out of 1,000 born	Mortality rate per thousand alive at beginning of interval	Expectation of life, or mean lifetime remaining to those attaining age intervals (years)
x	x'	d_x	l_x	$1000q_x$	e_x
0-1	-100	550	1,000	550	2.07
1-2	-52	202	450	449	1.87
2-3	-3	72	248	290	1.99
3-4	+45	60	176	341	1.60
4-5	+93	60	116	517	1.18
5-6	+142	38	56	678	0.90
6-7	+192	13	18	722	0.75
7-8	+237	5	5	1,000	0.50

by Deevey (1947). From this a survivorship curve has been constructed (text-fig. 7). The mortality rate in the first year of growth is moderately high (55%). It then declines to 30% by the third year. The sharp increase in mortality rate after the fourth year is due to human predation, as the clams attain marketable size. Without the interference of man, the Pismo Clam may occasionally reach the considerable age of 35 years or more, that is, about 800% positive deviation from the mean life span of the clam population subjected to the census.

There is a moderate amount of information available on mortality rates within the first year of growth of bivalve species and some instances will be given of this. Hancock and Simpson (1961) recorded a mortality rate of 66% for a population of *Cardium edule*, taken from one October to the next. Ansell (1961) determined a rate of 40% for *Venus striatula* in Kames Bay, Millport. Weymouth *et al.* (1925) studied the mortality of *Siliqua patula* following a heavy spatfall in the summer of 1923. The mortality rate from August to December was approximately 66% but a heavy winter storm caused widespread destruction, and the mortality rate calculated from August to February was 98%. Ford (1925) also recorded a high mortality rate of 89% from July to February for a *Spisula elliptica* population in Plymouth Sound. Gutsell (1930) observed that mortality in the bay scallop of American Atlantic shores is normally very high at sizes less than 10 mm.

At times of extremely high spatfall, the mortality can be enormous. Thus Smidt (1951) recorded a case of *Mya arenaria* in the Danish Waddensee, in which, of 43,000 estimated

spat successfully settled in June, none was left in the following October. Wilson (1965) gave further examples of very high first-year mortality. The data of Craig and Hallam (1963) suggest fairly low first-year mortality for a population of *Mytilus edulis* and fairly high mortality for a population of *Cardium edule*.



TEXT-FIG. 7. Survivorship curve for the Pismo Clam, *Tivela stultorum*.

Information is sparse on mortality rates after the first year. The data on *Tivela stultorum* suggest a gradually declining rate which might have continued for a considerable period but for the interference of man. The *Venus striatula* population studied by Ansell apparently had a rate of about 33% in the second and third years. In the case of the scallop *Placopecten magellanicus* the annual rate may drop as low as 10% after several years of growth (Merrill and Posgay 1964). On the other hand, Weymouth *et al.* (1931) deduced a gradually increasing mortality rate after the first year of growth of *Siliqua patula*. It

appears that, after the heavy first-year mortality in the case they studied, the rate dropped to negligible proportions for the next year or two, before increasing subsequently.

Clearly, in view of the present state of knowledge, it would be unwise to risk broad generalizations, apart from the presumption that first-year natural mortality is usually higher than in subsequent years, at least when spatfall is heavy. This is not surprising, since young bivalves are more prone to removal from the sediment by strong water movements. This renders them more vulnerable to predators or to the vicissitudes of the physical environment. Winter storms may therefore take a heavy toll. Certain predators such as flatfish only attack young and comparatively small bivalves of a given species, though others, such as carnivorous gastropods, are less discriminating. The latter, however, do not destroy the shells. The importance of population density is not yet clearly established. Intensive competition for food should result in high mortality, but whereas some data appear to support this, it is seemingly contradicted in other cases (Savage 1956, Ansell 1961).

In view of the wide fluctuations that take place in living populations, deductions of fossil mortality rates will depend on the elimination as far as possible of other variables. The next section deals with one of these.

EXPERIMENTS ON SHELL BREAKAGE

As both shell assemblages contain large proportions of fragments one is naturally led to investigate the possibility that certain size grades are more susceptible to destruction by physical agents than others (though obviously many fragments must be the result of fish and bird predation). If so this will clearly have a modifying effect on the size-frequency distributions.

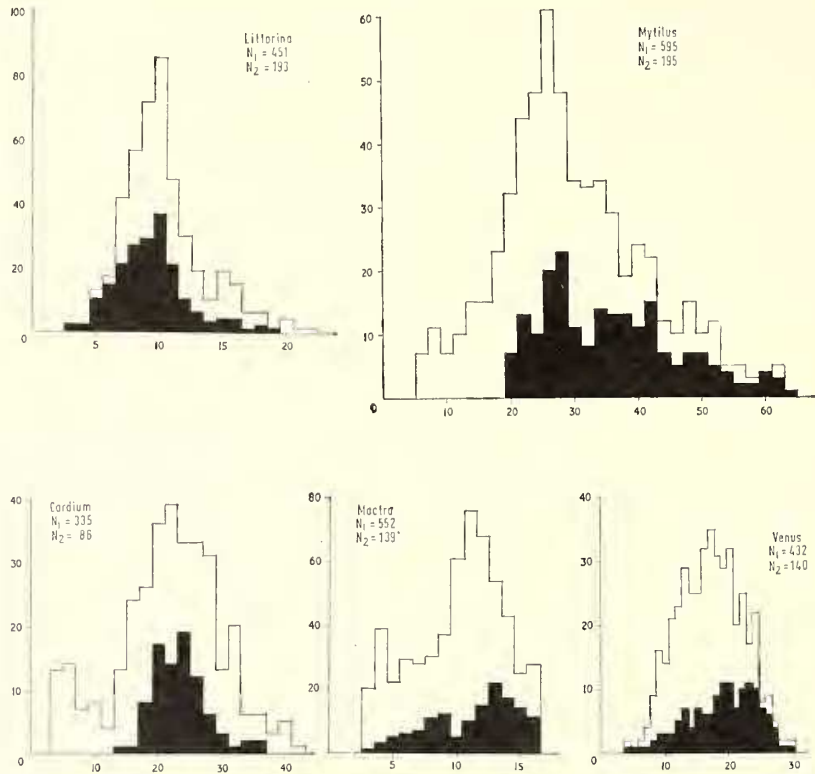
Experiments on shell breakage were undertaken with four of the commonest species in Gosford Bay, the bivalves *Cardium edule*, *Mytilus edulis*, and *Venus fasciata*, which between them represent a wide range in shape, and the gastropod *Littorina littorea*. The bivalve samples were collected over a wide area and no significance should be read into the size-frequency distributions portrayed in text-fig. 8. The *Littorina* sample, on the other hand, comes from the analysed assemblage, from which it was excluded because of the likely presence of small quantities of two other species of similar shape. The sample is readily acceptable for the experimental work, however.

The shells of each species, following size measurements, were in turn subjected to rapid tumbling in a closed container using a Turbula mixer-pulsator.

Periodic inspection was undertaken to determine when a substantial proportion of the shells had been fragmented. Shell destruction proved easily determinable with the bivalves, whose numbers were considerably reduced after a few minutes. The gastropods proved far more resistant because of the greater strength of coiled and relatively thick shells as opposed to shallow convex valves. The criterion used to determine destruction was puncture of the early whorls or complete removal of the apertural lip (clearly the criterion of destruction need only be consistent for one observer). Even this relatively modest damage took several hours to be accomplished, with tumbling at the same speed as with the bivalves.

The results (text-figs. 8 and 9) show pronounced differences between the behaviour of the bivalve and gastropod shells. The smaller shells of the bivalves are clearly more

susceptible to destruction in the experimental conditions, presumably because of their thinner shells. This is most strikingly shown in the case of the weakest shells, those of *Venus fasciata*. As illustrated in text-fig. 8, the histogram mode of the 'survivors' has shifted appreciably to the right and the shape has changed from symmetrical to negatively skewed. In the case of *Mytilus* and *Cardium* the modes have shifted only slightly to the right but all *Mytilus* shells less than 19 mm. and *Cardium* shells less than 12 mm.

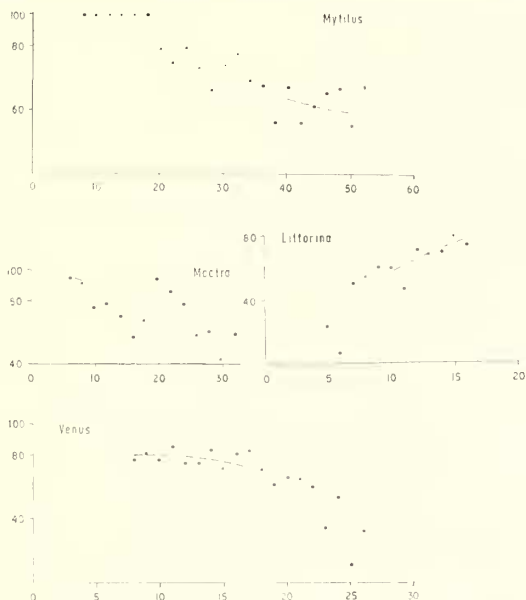


TEXT-FIG. 8. Size-frequency distributions of intact molluscan shells before (N1) and after (N2) breakage experiments. Size in mm.

long have been destroyed. With *Littorina*, in contrast, the smaller shells appear to be the more resistant. It will be seen from text-fig. 8 that the mode was unchanged after several hours and the general shape of the size-frequency histogram not appreciably altered.

It would have been futile to attempt to simulate natural conditions in the sea and it may be objected that small shells, with their different hydrodynamic properties, would not be subjected to crushing between larger shells as in the conditions of the experiment. In the absence of precise information on the actual mechanism of post-mortem shell fragmentation on the shore or elsewhere this can neither be refuted nor accepted. There is, however, some empirical evidence to suggest the existence of a selective fragmentation process among bivalves in natural conditions comparable to that observed in the experiments. In a study of the production of *Macra stultorum* in the western part of the

Dogger Bank, Birkett (1959) paid attention to the quantity of dead shells in the samples collected on successive cruises, showing an interest (exceptional among marine biologists) in the rate at which such shells break up once they have become empty. Data from Birkett's table 3 have been used in text-figs. 8 and 9. The larger histogram of text-fig. 8 represents a collection made in October 1958 and the smaller histogram one made in the following May, 218 days later. The numbers of unbroken shells were considerably reduced during this period, with the smaller, thinner shells being more readily destroyed, just as in the experiments described. No doubt winter storms played a major role in this



TEXT-FIG. 9. Data of text-fig. 8 plotted as percentages of broken shells of given species at different sizes.

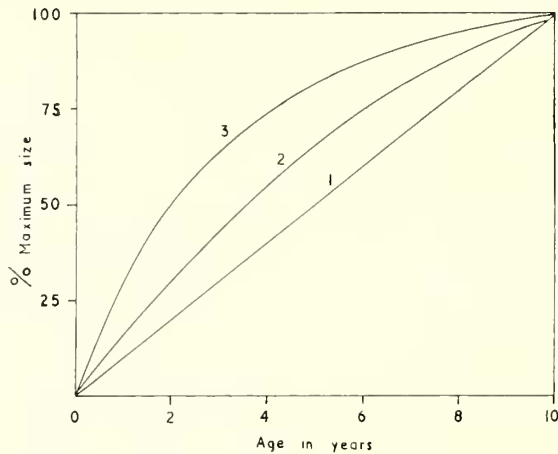
destruction. To Birkett it was evident that the smallest length classes of *Mactra* could not have survived for more than a few weeks in the ground. Schäfer (1962, p. 550) confirmed that a large proportion of bivalve shells do not survive in the North Sea beyond a few months after they become empty. Evidently, given conditions of agitated water, the factor of differential break-up of bivalve shells of different size grades cannot readily be discounted.

INTERPRETATION OF SIZE-FREQUENCY DISTRIBUTIONS

It was demonstrated in a previous study (Craig and Hallam 1963, text-fig. 8) that, given linear growth, constant mortality can be represented by a size-frequency histogram of the death assemblage rising at an increasing rate towards the origin, the mode being determined only by the size of the class interval chosen, while a constantly increasing mortality rate could give rise to an approximately normal distribution. Slight modifications result from the more realistic application of growth rate declining with time. Thus the normal distribution may become negatively skewed. It is obvious that age-frequency data, and hence approximate mortality rates, can only be derived from size-frequency

data provided the average growth rate of the assemblage under consideration can be worked out from growth rings. Unfortunately, this is not a practicable proposition for many molluscs, including most of the species under consideration. Reasonable approximations are obtainable, however, if realistic models of growth and mortality rates are constructed from existing data.

Three model bivalve growth curves are presented in text-fig. 10, one representing simple linear growth, which is approximated by some bivalves for parts of their life history; the second a growth characterized by a slow (approximately exponential) rate of change, half the maximum size (attained at 10 years) being achieved at $3\frac{1}{2}$ years; and



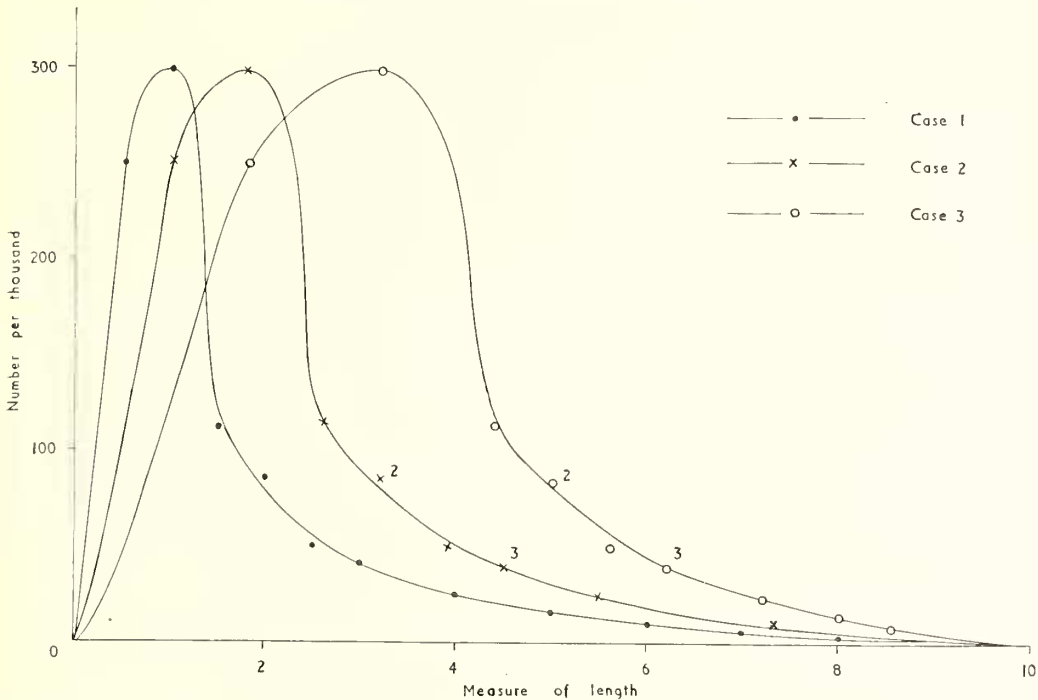
TEXT-FIG. 10. Three growth models for bivalves; case 1, simple linear growth; case 2, slow exponential decline; case 3, rapid exponential decline.

the third a growth characterized by a rapid rate of change, half the maximum size being reached at 2 years. These curves are, of course, simplifications but are satisfactory for the present purpose. The three curves seem to embrace reasonably adequately the documented cases of bivalve growth curves illustrated in text-fig. 6.

Producing a realistic mortality model is far more difficult, because of the lack of data and the wide fluctuations in mortality rate that are known to occur. It is considered soundest here to construct a model closely approximating to the mortality rates worked out for *Tivela stultorum* in the previous section, but taking into account that mortality among the first-year population is likely to be highest in the second half year of growth because of winter storms and cold spells. This can be achieved by taking 50% as the mortality rate for the first half-year, 80% for the next, 50% for the following two half-years, and 40% each subsequent half-year. This gives a 55% mortality rate for the first year, 45% for the second, and 36% for the third. Such a mortality distribution must indeed approximate a large number of actual cases, judging from the data which exist.

In text-fig. 11 size-frequency distributions are given using this mortality model and the three growth models of text-fig. 10. The influence of widely varying initial growth rates is clearly shown and needs no comment, but it should be observed that each curve has a long tail to the right. Such tails are the inevitable result of mortality rates which do not increase notably with time, and is almost certainly the normal situation.

Returning now to the two shell assemblages illustrated in text-figs. 1 to 4, it becomes readily apparent that the *general* shapes of the size-frequency histograms must be primarily due to the interaction of fairly normal growth and mortality rates. Those with strong positive skewness signify high juvenile mortality rate, with a subsequent decline, while the few with symmetrical distributions could signify a condition of increasing mortality with time, or a high initial growth rate, or a combination of the two (obviously, independent growth data are required to decide between these alternatives).



TEXT-FIG. 11. Size-frequency distributions derived from the three growth models of text-fig. 10 and a mortality model described in the text, based on data from *Tivela stultorum*.

There is a strong suggestion that there has been selective removal of small shells, however, in at least some cases, because the approximate mortality rates that may be deduced from the histograms do not appear to correspond sufficiently closely with the more directly derived data reviewed earlier, which indicate high rates of juvenile mortality as the common condition. This difference is brought out clearly in text-fig. 5. In the case of the bivalves at least (to which may be added with reasonable confidence the thin-shelled limpet *Crucibulum*, though not the coiled gastropods *Olivella* and *Littorina*), there is a ready explanation available, namely selective fragmentation in an agitated aqueous environment. While such fragmentation has in all likelihood removed a considerable proportion of the smaller shells, it is unlikely that it has succeeded in doing more than altering the degree of skewness. It certainly cannot explain the rarity of small specimens of, for instance, *Pseudochama* and *Tivela* in the Newport Bay sample, which must be largely attributable to low juvenile mortality. Nor can it account for the virtual absence of small *Ensis* shells in the Gosford Bay sample. This must principally

be due to an exceptionally high initial growth rate compared with the smaller-sized species, together with only slight mortality during the first few months of growth. Lack of information about mortality in the period just after settling of spat, and about growth rates in specific cases, provide limits to the confidence of interpretation.

None of this proves, of course, that size sorting has played no role whatever, but its invocation appears unnecessary and the burden of proof in these and similar cases rests squarely upon those who would insist upon its importance. It is not sufficient to reiterate the obvious, that shells of different size and thickness have different hydrodynamic properties. In régimes subjected to tidal action, for instance, oscillating currents are likely to return what they have removed, and the net effect may be negligible. Even in cases in which a size-sorting effect has been experimentally demonstrated, the results may not be readily predictable. Thus Lever *et al.* (1964) found that large valves of *Donax vittatus* are actually transported more readily than small valves.

DISCUSSION

Although information is unfortunately insufficient for the rigorous disentanglement of the several variables involved, it can be claimed with reasonable confidence that the present study lends little support to the hypothesis that size-frequency distributions of transported and highly disturbed shell assemblages primarily reflect size sorting, but are rather the result of the interaction of normal growth and mortality rates, somewhat modified in all probability by the selective destruction of smaller shells.

The Newport Bay Pleistocene assemblage may represent a strandline accumulation like the Gosford Bay assemblage, and consists of fossils which in life inhabited intertidal or shallow subtidal waters. Accumulation on the strandline is, together with the formation of lag concentrates in channels, by far the most important way of forming transported shell concentrations around our present shores. It is apparent from the work of Schäfer and others that the duration of complete shells in a disturbed aqueous environment is limited to brief periods in most cases, and assemblages such as those described are most probably the result of only a few years of growth; in the case of species with small fragile shells they may represent only one year of growth.

In reply to the contention that because most strandline accumulations are destroyed quickly they are insignificant in the fossil record it may be pointed out that they have a chance of preservation comparable with ripple marks or similar 'transient' sedimentary structures. A certain proportion of such shell beds must be preserved following ultimate burial of a sedimentary accumulation of the appropriate type.

Fossils are often concentrated, of course, as a result of slow sedimentation. Condensed shell beds formed in this way should exhibit wider scatter in the size-frequency distributions of their component species, because of the mixing of forms which grew at varying speeds at widely differing times. Diagenetic solution of small, thin shells is more likely to be of importance in this type of shell bed than any other. If the selective destruction of small, thin shells in agitated water is a major factor then argillaceous deposits should contain higher proportions of juveniles than arenaceous ones. Black shales usually signify deposition in stagnant or near-stagnant water in which water disturbance was at a minimum. Such deposits frequently contain minute shells of given species which have been widely interpreted, with some justification, as stunted adults (Hallam 1965).

A condition of declining mortality rate with age, combined with lack of selective destruction, may give rise to a strong juvenile peak and a very small number of much larger adults. Unless large samples are collected, of the order of hundreds of specimens for each species, these adults may easily be missed. It is clearly desirable to undertake thorough size-frequency analyses of a number of species in a fauna when stunting is suspected.

Acknowledgement. I am indebted to Dr. G. Y. Craig for his helpful comments.

REFERENCES

- ANSELL, A. D. 1961. Reproduction, growth and mortality of *Venus striatula* (da Costa) in Kames Bay, Millport. *J. mar. biol. Ass. U.K.* **41**, 191–215.
- BIRKETT, L. 1959. Production in benthic populations. *Internat. Council for Exploration of Sea: Near Northern Seas Committee*, no. 42, 1–12.
- BOUCOT, A. J. 1953. Life and death assemblages among fossils. *Am. J. Sci.* **251**, 25–40.
- BROADHURST, F. M. 1964. Some aspects of the palaeoecology of non-marine faunas and rates of sedimentation in the Lancashire Coal Measures. *Ibid.* **262**, 858–69.
- COE, W. R. and FOX, D. L. 1944. Biology of the California sea mussel (*Mytilus californianus*). III. Environmental conditions and rate of growth. *Biol. Bull. mar. biol. Lab., Woods Hole*, **87**, 59–72.
- CRAIG, G. Y. and HALLAM, A. 1963. Size-frequency and growth-ring analyses of *Mytilus edulis* and *Cardium edule*, and their palaeoecological significance. *Palaeontology*, **6**, 731–50.
- DEEVEY, E. S. 1947. Life tables for natural populations of animals. *Q. Rev. Biol.* **22**, 283–314.
- FAGERSTROM, J. A. 1964. Fossil communities in paleoecology: their recognition and significance. *Bull. geol. Soc. Am.* **75**, 1197–216.
- FITCH, J. E. 1950. The Pismo Clam. *Calif. Fish Game*, **36**, 285–312.
- FORD, E. 1925. On the growth of some lamellibranchs in relation to the food supply of fishes. *J. mar. biol. Ass. U.K.* **13**, 531–59.
- GUTSELL, J. S. 1930. Natural history of the bay scallop. *Bull. Bur. Fish. Wash.* **46**, 569–627.
- HALLAM, A. 1965. Environmental causes of stunting in living and fossil marine benthonic invertebrates. *Palaeontology*, **8**, 132–55.
- HANCOCK, D. A. and SIMPSON, A. C. 1961. Parameters of marine invertebrate populations. In: *The Exploitation of Natural Annual Populations*. Ed. E. D. LE CREN and M. W. HOLDGATE, Oxford.
- HOPKINS, H. S. 1930. Age differences and the respiration in muscle tissues of mollusks. *J. exp. Zool.* **56**, 209–39.
- LEVER, J., VAN DEN BOSCH, M., COOK, H., VAN DIJK, T., THIADENS, A. J. H., and THUISSEN, R. 1964. Quantitative beach research: III. An experiment with artificial valves of *Donax vittatus*. *Neth. Jnl Sea Res.* **2**, 458–92.
- MASON, J. 1957. The age and growth of the scallop, *Pecten maximus* (L.), in Manx waters. *J. mar. biol. Ass. U.K.* **36**, 473–92.
- MERRILL, A. S. and POSGAY, J. A. 1964. Estimating the natural mortality rate of the Sea Scallop (*Placopecten magellanicus*). *Bull. Int. Comm. North West Atlantic Fish. Res.* **1**, 89–106.
- NEWCOMBE, C. L. 1935. Growth of *Mya arenaria* L. in the Bay of Fundy region. *Can. J. Res.* **13**, D, 97–137.
- OLSON, E. C. 1957. Size-frequency distributions in samples of extinct organisms. *J. Geol.* **65**, 309–33.
- ORTON, J. H. 1926. On the rate of growth of *Cardium edule*. Part 1. Experimental observations. *J. mar. biol. Ass. U.K.* **14**, 239–79.
- SAVAGE, R. E. 1956. The great spatfall of mussels (*Mytilus edulis* L.) in the River Conway estuary in Spring, 1940. *Fishery Invest., Lond., Ser. 2*, **20**, 7. H.M.S.O.
- SCHÄFER, W. 1962. *Aktuo-Paläontologie nach Studien in der Nordsee*. Frankfurt a. M.
- SMIDT, E. L. B. 1951. Animal production in the Danish Waddensee. *Meddr Konunnu Danu. Fisk.-og. Havunders., Ser. Fisk.* **2**, no. 6.
- VOGEL, K. 1959. Wachstumsunterbrechungen bei Lamellibranchiaten und Brachiopoden. *N. Jb. Geol. Paläont., Abh.* **109**, 109–29.

- WEYMOUTH, F. W. 1923. The life history and growth of the pismo clam (*Tivela stultorum* Mawe). *Calif. Fish Game Commiss., Fish. Bull.* 7.
- MCMILLIN, H. C. and HOLMES, H. B. 1925. Growth and age at maturity of the Pacific razor clam, *Siliqua patula* (Dixon). *Bull. Bur. Fish., Wash.* 41, 201–36.
- — and RICH, W. H. 1931. Latitude and relative growth in the razor clam, *Siliqua patula*. *J. exp. Biol.* 8, 228–49.
- and THOMPSON, S. H. 1931. The age and growth of the Pacific cockle (*Cardium corbis* Martyn). *Bull. Bur. Fish., Wash.* 46, 633–41.
- WILSON, J. B. 1965. The palaeoecological significance of infaunas and their associated sediment. *Unpubl. Ph.D. Thesis, Univ. Edinburgh.*

A. HALLAM
Grant Institute of Geology,
King's Buildings,
West Mains Road,
Edinburgh 9

Manuscript received 18 November 1965